

NEW OBSERVATIONS ON THE ECOLOGY OF THE PERMIAN CAPITAN REEF, TEXAS AND NEW MEXICO

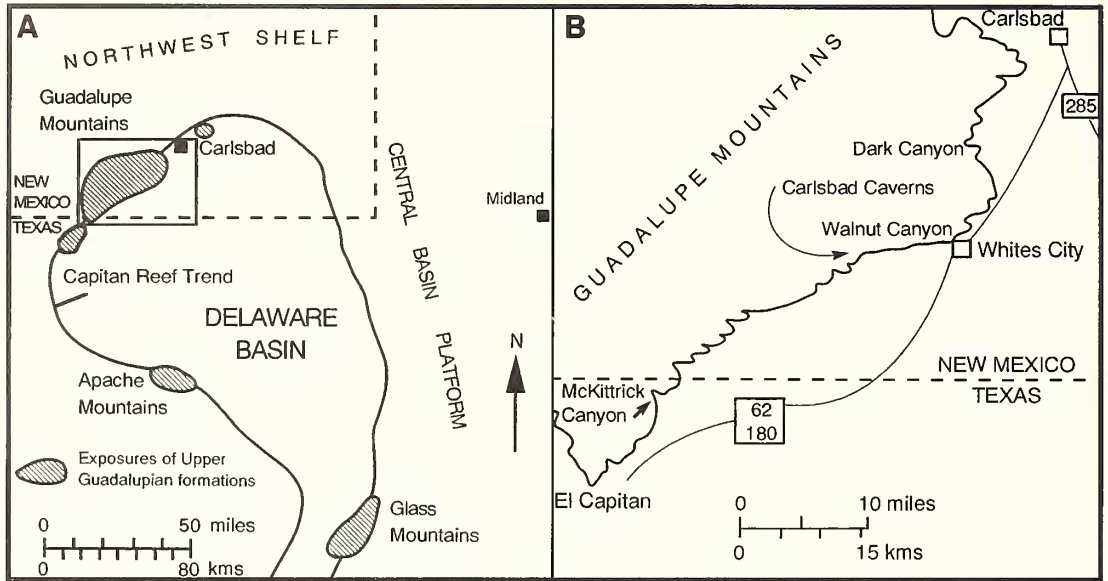
by RACHEL WOOD, J. A. D. DICKSON *and* BRENDA L. KIRKLAND

ABSTRACT. The Permian Capitan reef was a predominantly heterotrophic ecosystem strongly differentiated into open surface and cryptic communities. Unlike modern phototrophic coralgal reefs, most of the preservable epibenthos was housed within the cryptos and zonation developed only in the shallow parts of the reef. Contrary to established opinion, most sphinctozoan sponges did not grow upright to form a baffling framework but rather were pendent cryptobionts, as were nodular bryozoans and rare solitary rugose corals and crinoids. Indeed, many members of the cryptos were obligate cryptobionts. Much of the Middle Capitan reef framework was constructed by a scaffolding of large frondose bryozoans, with the subsidiary platy sphinctozoan *Guadalupia zitteliana*. Bathymetrically shallow areas of both the Middle and Upper Capitan reef, however, were characterized by platy sponges. In parts of the Upper Capitan, some platy sponges (*Gigantospongia discoforma*) reached up to 2 m in diameter and formed the ceilings of huge cavities which supported an extensive cryptos.

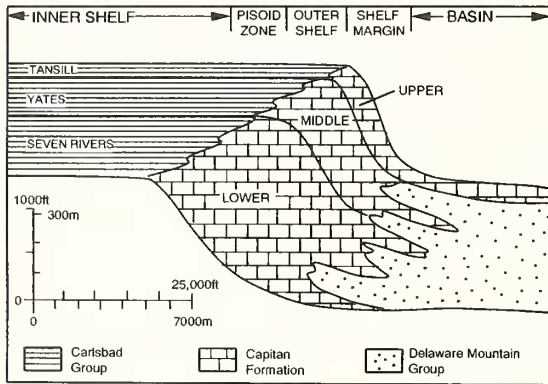
In the absence of destructive forces (both biotic and physical) prevalent on modern reefs, the relatively fragile Capitan reef remained intact after the death of the constructing organisms. Rigidity was imparted to this community by a post-mortem encrustation of *Tubiphytes* and *Archaeolithoporella*, together with microbial micrite. The resultant cavernous framework was partially infilled with sediment and preserved by syndimentary intergrowth of aragonitic botryoids and *Archaeolithoporella*. Extensive cement precipitation was favoured by a number of factors including deep anoxia, which generated upwelling waters with elevated alkalinity. Although the accumulation rate of the Capitan may have been comparable to that of modern coralgal reefs, both the trophic structure and relative contributions of inorganic and organic carbonate were profoundly different.

CALCIFIED metazoans have aggregated to form reefal buildups throughout the Phanerozoic, but during this time many evolutionary innovations as well as extinction events have exerted profound changes on the biotic constituents and trophic structure of reef communities. Modern coralgal reefs are highly complex, specialized ecosystems driven by photosymbiosis and regulated by intense predation. Yet there is little evidence (except possibly in tabulate corals) for the existence of widespread photosymbiotic reef communities before the acquisition of zooxanthellae by scleractinian corals in the late Triassic (Wood 1993). Moreover, most predator groups responsible for the regulation of modern reef community structure did not appear until the late Mesozoic or early Cenozoic (Wood 1993, 1995). We can therefore expect Palaeozoic reefs to have had a very different ecological caste to modern representatives.

The Permian Capitan reef, West Texas and New Mexico, forms one of the finest examples of an ancient rimmed carbonate shelf. The reef, as expressed in the massive Capitan Limestone (Hayes 1964) and associated upper Guadalupian carbonate platform, defines the margin of the Delaware Basin (Text-fig. 1). Equivalent shelf units form reservoirs on the northern and eastern sides of the basin (Ward *et al.* 1986). Although most of the Capitan reef is subsurface, spectacular exposures are known from the Guadalupe, Apache, and Glass Mountains. The east side of the southern Guadalupe Mountains represents an erosionally modified depositional profile of shelf to basin sediments which were exhumed during the late Cenozoic, with the reef itself marking a prominent



TEXT-FIG. 1. A, map of the Permian Delaware Basin showing exposures of upper Guadalupian formations and location of the Capitan reef trend; B, detail of the Capitan reef front, Guadalupe Mountains with locations mentioned in the text (modified from King 1948).



TEXT-FIG. 2. Schematic cross section showing shelf-to-basin correlations of the Capitan Formation and equivalents (after Babcock and Yurewicz 1989) and subdivision of the shelf (after Esteban and Pray 1983).

topographical boundary between deep-water basinal deposits and shallow shelf sediments to the north-west.

During the Late Permian, the Delaware Basin was almost entirely surrounded by land (Ward *et al.* 1986) and lay a few degrees north of the equator on the western side of Pangaea (McKerrow and Scotese 1990). The area was intermittently arid, as evidenced by large evaporite deposits in the basin and its fringing lagoons (Adams and Rhodes 1960). Indeed, the basin and shelf deposits of the Delaware Basin were sealed and preserved by latest Permian (Ochoan) evaporites.

The Capitan reef is the youngest of a series of shelf-margin complexes which developed around the Delaware Basin over a total period of some 12 My (Garber *et al.* 1989). The reef forms prograding beds of generally 20–40°; but which may locally be vertical (Bebout and Kerans 1993).

These massive limestones served to mark an abrupt transition between the basin floor and shelf which has been suggested to have progressively shallowed (Cys 1971; Babcock 1977; Toomey and Babcock 1983): by the end of Capitan Limestone deposition water depth in the Delaware Basin is estimated to have reached 450–600 m (Yurewicz 1976). There is also an abrupt contact between the massive limestones and the bedded grainstones and packstones of the outer shelf (Text-fig. 2). These shelf sediments contain a biota characteristic of restricted, slightly hypersaline conditions and their mud content increases shelfwards suggesting quiet, back-reef lagoonal deposition (BLK, pers. obs.).

Classic exposures of the Capitan reef and its associated sediments are known from a series of canyons running parallel and perpendicular to the reef-margin. Some canyons, such as McKittrick, display nearly complete sections through the platform margin, thus allowing interpretation of both the changing depositional profile and the nature of the transition from the reef to associated sediments. Notwithstanding such excellent exposure, however, many aspects of the nature of the reef margin have remained enigmatic. The crucial facies which controlled sedimentation across the late Guadalupian shelf margin is the massive Capitan Limestone, yet little is known as to its mode or depth of formation. The Capitan Limestone may also have controlled deposition of the shelfward lithologies of the Carlsbad Group (Seven Rivers, Yates and Tansill formation; BLK, pers. obs.).

The Capitan Limestone ranges from 100–200 m thick and has been subdivided into Lower, Middle and Upper members (Babcock 1977; Yurewicz 1977) equivalent to the Seven Rivers, Yates and Tansill formations respectively (Text-fig. 2). The Capitan Limestone contains a diverse and distinctive biota estimated at some 350 taxa (Girty 1908; King 1948; Newell *et al.* 1953; Fagerstrom 1987), which includes abundant calcareous sponges (the polyphyletic chambered spinozoans and non-chambered inozoans), putative algae, bryozoans, brachiopods and several enigmatic organisms such as *Tubiphytes*. Interpretations as to whether any of these organisms were capable of producing a wave-resistant framework have remained at the heart of the Capitan controversy. Workers who consider a rigid framework to have been present compare the Capitan to a modern coralgal barrier reef (Crandall 1929; Lloyd 1929; Johnson 1942; Newell *et al.* 1953; Newell 1955; Klement 1966; Cys 1971; Cronoble 1974; Yurewicz 1977; Mazzulo and Cys 1978; Fagerstrom 1987; Babcock and Yurewicz 1989; Kirkland-George 1992; Kirkland *et al.* 1993). In contrast, Achauer (1969) and Dunham (1970, 1972) proposed the Capitan Limestone to have formed as a linear bank of baffling metazoans growing in deeper waters. They considered that few fossils are in growth position and therefore inferred that the community was incapable of creating a wave-resistant framework. Others have emphasized the constructional role of extensive algal encrustation and early cementation in producing a rigid framework which bore considerable relief (Babcock 1974, 1977; Yurewicz 1976, 1977; Schmidt 1977; Mazzullo and Cys 1978).

Interpretations as to the depth at which the Capitan Limestone formed are critical to late Guadalupian physiography, but remain a matter of intense controversy. Such uncertainty is exemplified by the number of competing bathymetric profile models proposed for the shelf margin. Newell *et al.* (1953) depicted a profile similar to a modern barrier-reef with the Capitan growing to sea-level. Dunham (1972) proposed the pisolite facies belt landwards of the reef to be a series of subaerially exposed shoals, whilst the reef grew below wave base and had little positive topographical relief. Kirkland (1992) included both exposed tidal flat facies and a reef growing to sea-level in her reconstruction of the shelf margin. These models cannot be reconciled: whether the reef formed in turbulent surface waters or in the more tranquil depths is of fundamental ecological importance.

METHODS

Detailed field observations of biotic interactions were made on naturally weathered surfaces parallel to reef growth on the Permian Reef Geology Trail, McKittrick Canyon which exposes approximately 140 m of the Middle Capitan Limestone (middle and upper Yates-equivalent). Acid-etched surfaces of approximately 43 m of upper Upper Capitan Limestone (lower Tansill-equivalent) were studied at the mouth of Walnut Canyon, Whites City. Hand specimens collected from both these localities were either serially slabbed and polished or thin sectioned. Additional

observations of reef fabrics were made in the Left Hand Tunnel of Carlsbad Canyon. The zone foraminifera *Polydioexodina* is found above these exposures indicating a lower middle Capitan or older age (BLK, pers. obs.).

Studied material has been lodged in the Sedgwick Museum, Cambridge (prefix SMX) and the Dept of Geology, University of Texas, Austin (prefix STC).

ECOLOGY

The massive Lower and Middle Capitan Limestone contains fewer putative algae than the Upper Capitan and has been interpreted to be a shelf-edge accumulation of various suspension feeders (especially calcareous sponges and bryozoans) living in moderately deep water of low turbidity (Yurewicz 1976, 1977; Babcock and Yurewicz 1989). Yurewicz concluded that the Middle Capitan Limestone exhibited 20–60 per cent. boundstone (the remainder being packstone and grainstone) in which he identified three distinct fabrics: two dominated volumetrically by the encrusting putative rhodophyte *Archaeolithoporella* and one by the problematical branching or encrusting ?alga *Tubiphytes*. Yurewicz proposed that all boundstone fabrics initiated upon erect skeletal organisms, which formed the framework for subsequent *Archaeolithoporella* encrustation and inorganic cementation. He believed that the Lower Capitan reef was 45 m deep at its crest, rising to 30 m by the end of Middle Capitan time. He found little evidence for zonation.

A further reef fabric in the Middle Capitan Limestone was identified along the Permian Reef Geology Trail, McKittrick Canyon: patchily developed thickets of *Tubiphytes* and *Acanthocladia* (a ramose bryozoan), with voids infilled with cement and laminated internal sediment (Kirkland *et al.* 1993). They noted the restriction of the ?alga *Collenella* to the shallowest parts of the reef – those nearest to the outer shelf. Apart from this observation, they also concluded that little zonation is evident in the Middle Capitan Limestone as exposed in the Permian Reef Geology Trail.

The Upper Capitan Limestone has been described as being dominated by abundant and diverse frame-building calcareous algae growing in intimate association with inorganic cement (Babcock 1974, 1977). Babcock concluded that a greater proportion of this upper part of the reef was in situ, with 50–75 per cent. boundstone fabrics. He identified four boundstone fabrics: *Collenella/Parachaetetes*, *Tubiphytes*, *Tubiphytes*-sponge and *Archaeolithoporella*/nodular. He concluded that the Upper Capitan grew to within 10 m of sea level, and showed marked algal zonation.

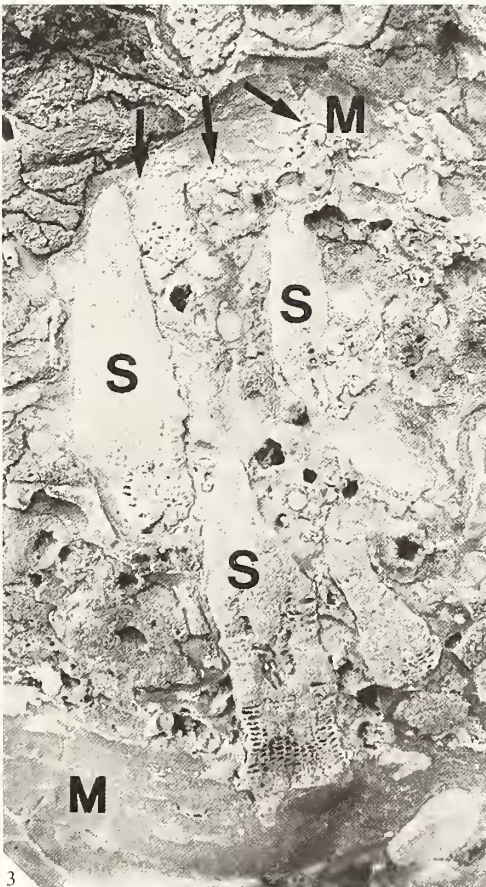
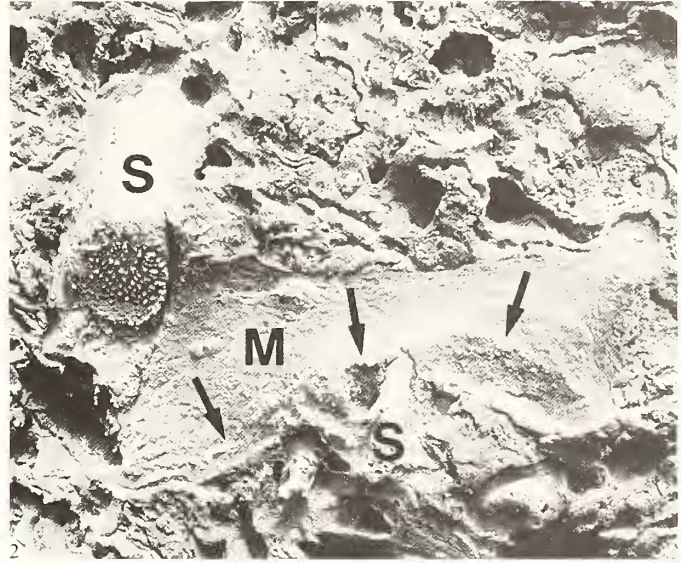
Established ecological reconstructions have thus emphasized the role of various baffling branching or solitary organisms (sphinctozoan sponges, bryozoans and *Tubiphytes*) and massive putative algae (*Collenella*, *Parachaetetes* and *Solenopora*) in the construction of the Capitan reef, together with the binding and encrusting contribution of *Archaeolithoporella* and extensive early marine cementation. Babcock and Yurewicz (1989) emphasized that cement growth was prolific, initiating not only within micropores and in large cavities below the surface of deposition, but also as crusts or nodules directly upon the sea floor.

EXPLANATION OF PLATE I

Frondose bryozoan-sponge community

Figs 1–4. Weathered surfaces parallel to reef growth from the Middle Capitan Limestone, McKittrick Canyon, showing latticework of bryozoans (arrowed) forming cavity boundaries which support a cryptos of sphinctozoan sponges (S). Note post-mortem encrustation of micrite (M). Remaining space is infilled by intergrown *Archaeolithoporella* and cement botryoids. Figs 1, 4, $\times 0.2$; Figs 2–3, $\times 1$.

Fig. 5. Weathered surface approximately perpendicular to reef growth showing bryozoan fronds (arrowed) clearly forming the framework for the subsequent precipitation of microbial micrite (M). Remaining cavity space has been infilled by late-stage sparry calcite; $\times 0.5$.



In this study we have identified five reef-building communities in the middle and upper Capitan Limestone. The (1), phylloid algal and (2), *Tubiphytes*-sponge communities of Babcock (1974, 1977) have been noted at the mouth of Walnut Canyon, Whites City between the elevations of 1130–1133 m and 1138–1143 m respectively. The (3), *Tubiphytes-Acanthocladia* community of Kirkland *et al.* (1993) was found in isolated patches throughout the Middle Capitan exposed at McKittrick Canyon, except in the uppermost 10 m of the reef. The most widespread reef fabrics encountered, however, represent two newly identified associations, here named the frondose bryozoan-sponge and platy sponge communities. They correspond in part to the previously described *Archaeolithoporella*-dominated communities (Babcock 1974, 1977; Yurwicz 1976, 1977; Babcock and Yurewicz 1989). Their distribution and ecology are described below.

Fronlose bryozoan-sponge community

This community has been identified from the Middle Capitan Permian Reef Geology Trail in McKittrick Canyon, where it forms the bulk of discernible reef fabric from the base of the Capitan Limestone exposure (at an elevation of approximately 1905 m) to within approximately 10 m of the uppermost exposure of the Massive Member (Hayes 1964) at some 2050 m elevation, giving a total thickness of some 130 m. The same association has been found within the Upper Capitan Limestone at the mouth of Walnut Canyon, Whites City, where it occurs at the base of the exposure some 30 m below the highest contact between the reef and backreef. A similar fabric was also noted in the fallen blocks from the Left Hand Tunnel of Carlsbad Canyon, which are thought to be of Lower or Middle Capitan age.

Contrary to established opinion, the vast majority of calcified sponges (sphinctozoans) found at these locations are cryptic, projecting downwards into cavities (Wood *et al.* 1994). Most sponges are attached to the upper surface of crypts (Pl. 1, figs 1–4), whilst a few project from the walls or floors. Where holdfast structures are discernible, the sponges are commonly attached to frondose bryozoans (Pl. 1, figs 1–4) identified as *Goniocladia* sp., two species of *Fenestella* and cf. *Polypora* sp., or occasionally to the platy sphinctozoan *Guadalupia zitteliana* (Pl. 2, fig. 1). Polished serial-slabs reveal the ceilings and walls of crypts often to be supported by these highly convoluted fan- or plate-shaped metazoans (Text-fig. 3). The pervasive nature of the primary constructional role of the frondose bryozoans in particular is demonstrated by the tracing of vertical weathered surfaces parallel to reef-growth (Text-fig. 4), where the bryozoans commonly demark ceilings and walls of large crypts up to 0.5 m wide and 0.4 m high. Bryozoan fronds appear to have grown in varied orientations and are up to 0.25 m in any one dimension. They often show secondary thickening and inter-colony fusion.

Fronlose bryozoans and *Guadalupia zitteliana* thus formed a community of erect, or horizontally projecting fans whose undersurfaces were colonized by an abundant cryptic epibenthos (Text-fig. 5A; Table 1). The preservable cryptos was dominated volumetrically by diverse solitary sphinctozoan sponges, especially *Lemonea cylindrica*, *Amblyliphonella* spp. and *Cystauletes* spp., which are commonly 50–100 mm long but may reach 200 mm. These sponges show some alignment, suggesting preferential growth possibly in response to prevailing current direction (Text-fig. 6). Small, nodular bryozoans (*Girtypora* sp. and *Fistulipora* spp.) up to 7 mm in diameter are also common crypt dwellers, and may be attached either directly to platy sponges or frondose bryozoans (Pl. 2, fig. 3), or to other cryptobionts. Rare, nestling small rugose corals, crinoid holdfast structures with associated stems and an unidentified massive encruster have also been identified within crypts (Table 1).

Much of the reef community shows evidence of multiple biological encrustation. Chains of pendent sphinctozoan individuals are common. Both the open surface community and cryptos are often covered by encrustations up to 40 mm thick of intergrown *Archaeolithoporella*, *Tubiphytes* and foraminiferans (Pl. 2, fig. 2), together with rare hexactinellids and weakly calcified encrusting sponges and soft-bodied encrusters (Pl. 2, fig. 1). There is also some evidence of microboring activity.

The metazoan reef community accounts for only a minor proportion of the total reef fabric, occupying approximately 7–17 per cent. of which 6–15 per cent. is occupied by the cryptic sponges. A substantial proportion of the reef fabric (25–50 per cent.) is now occupied by pale to mid-grey laminated micrite. This material has previously been interpreted as geopetal detrital sediment infill (Babcock 1974, 1977; Babcock *et al.* 1977; Kirkland *et al.* 1993). Close inspection, however, reveals that micrite occurs not only as cavity fill but also as an encrustation around the open-surface community (Pl. 1, figs 2–3, 5) and pendent cryptos (Pl. 1, figs 2, 4). The micrite has a layered, thrombolitic to peloidal texture in thin section (Pl. 2, fig. 4), and incorporates bioclastic debris. It is commonly encrusted by multiple generations of foraminifers (Pl. 2, fig. 4). The absence of an organic cellular texture and the incorporation of detritus implies a soft, mucoidal precursor rather than a rigid skeletal structure. We suggest this micrite to be of microbial origin (Wood *et al.* 1994) which grew incrementally and became lithified syndepositionally. On the basis of its enveloping distribution around many skeletal elements of the reef fabric, this microbial micrite encrustation is proposed to have occurred after the death of the encrusted biota. The micrite would have served to lend considerable rigidity to an otherwise relatively fragile reef framework, forming an open network of interconnected cavities and tunnels.

Remaining cavity space (up to approximately 70 per cent.) was infilled by assorted bioclastic sediment, botryoids and intergrown *Archaeolithoporella*, botryoids and various late stage spars (Mruk 1989). Botryoids form grey and brown fans 10–50 mm in radius and nucleated on crypt ceilings, walls and floors as well as from the projecting cryptos (Pl. 2, fig. 1). Petrographic and isotopic analysis suggests an aragonitic precursor and marine origin (e.g. Loucks and Folk 1976; Mazzullo and Cys 1979; Mruk 1985, 1989). Several generations of isopachous radial calcite rimming cements 0.5–4 mm thick also encrust the surfaces of pendent cryptos and botryoids, postdating botryoid growth (M. Rahnis and BLK, pers. obs.). Remaining cavity space was infilled by various dolomites, late-stage sparry calcites, evaporite minerals and kaolinite (Scholle *et al.* 1992).

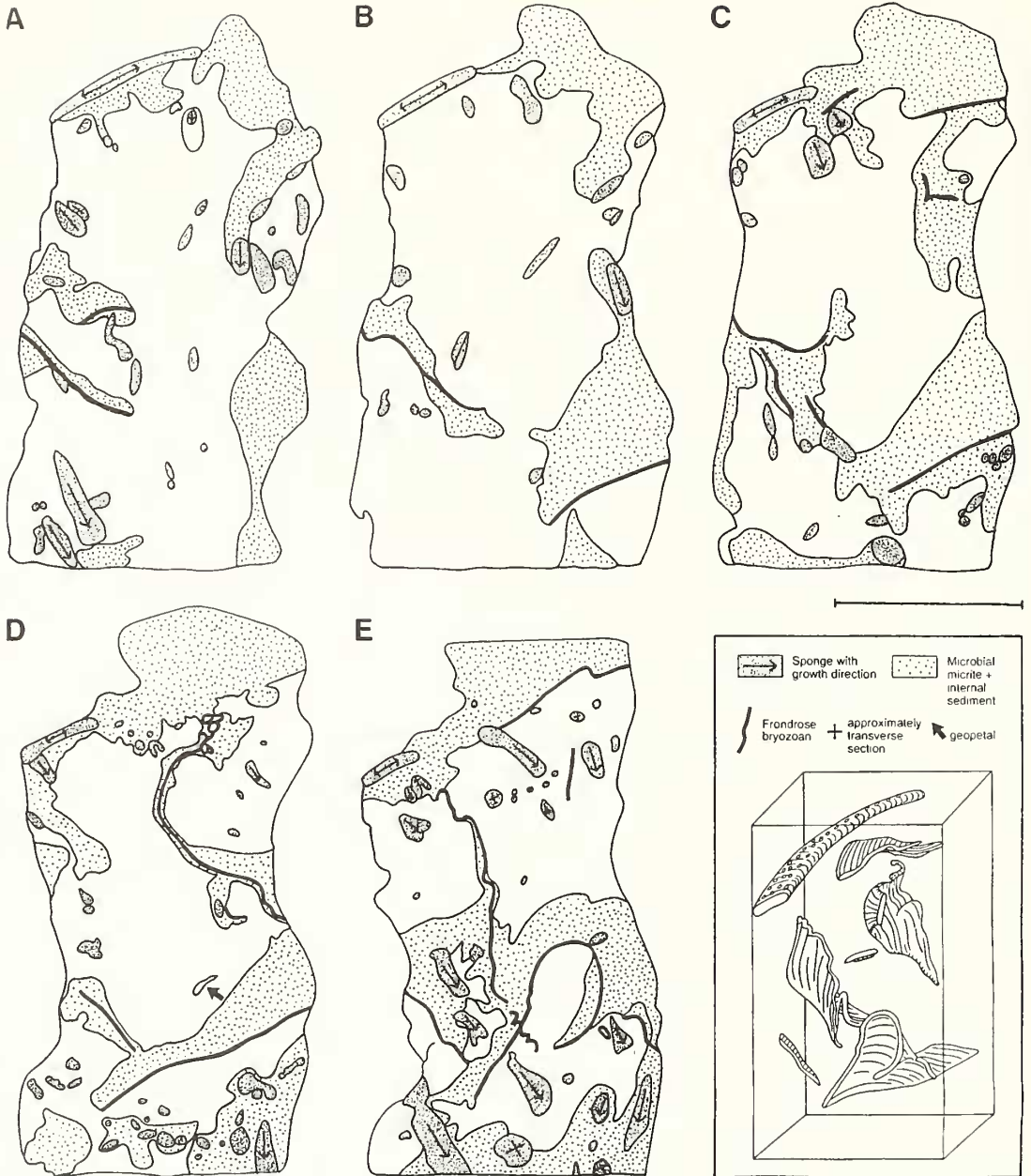
From these observations we infer the sequence of development of the frondose bryozoan-sponge community to have been:

1. Inter-connected large, convoluted fan-shaped bryozoan colonies and the platy sphinctozoan *Guadalupia zitteliana* grew projecting from the reef together with small thickets of branching acanthocladid bryozoans and *Tubiphytes* (Text-fig. 5A).
2. The undersurfaces of these platy metazoans formed open crypts which were colonized by an abundant biota dominated by pendent sphinctozoan sponges and small bryozoans.
3. The cryptos was encrusted by foraminiferans, *Tubiphytes* and *Archaeolithoporella*.
4. The entire epibenthic community was encrusted post-mortem by microbial micrite forming a rigid, open framework.
5. Cavity space was initially filled by sediment and the syn-sedimentary intergrowth of aragonitic botryoids and *Archaeolithoporella*, with the bulk of remaining space filled by botryoids. Some cavities remained entirely open.

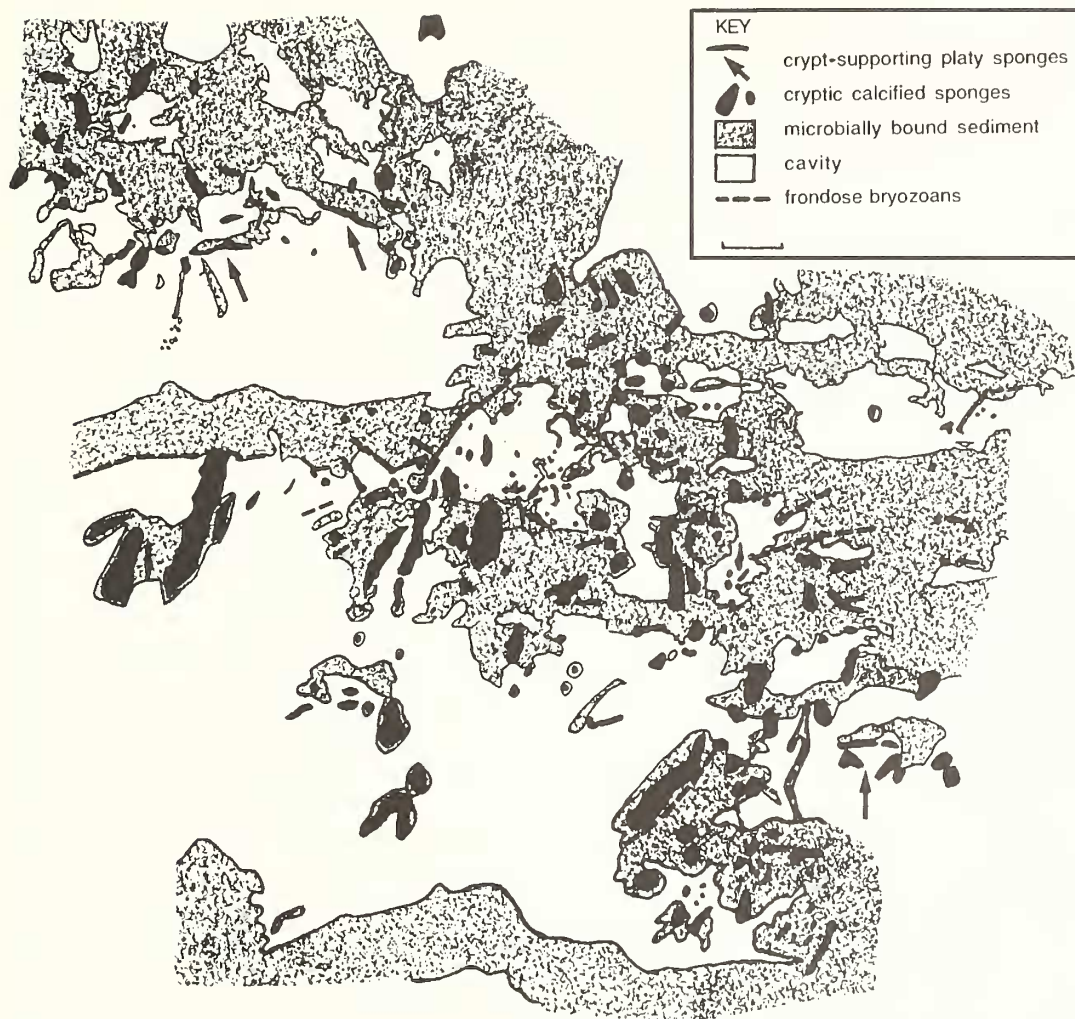
Platy sponge community

A community dominated by platy sponges has been identified from the upper 10 m of the Middle Capitan reef on the Permian Reef Geology Trail, McKittrick Canyon (2050–2060 m elevation) and in fallen blocks within the reef foreslope thought to be equivalent to the Upper Capitan (Bebout and Kerans 1993). The platy sponges are the sphinctozoan *Guadalupia zitteliana*, which develops a convex morphology and may reach up to 0.25 m in diameter (Pl. 4, figs 1, 4). This community is associated with rare, small erect growths (up to 0.15 m high) of *Collenella*.

A further platy sponge community is well developed in the lower Upper Capitan Limestone between the elevations of 1133–1138 m (i.e. 10–5 m below the topmost exposure of the Capitan Limestone) at Walnut Canyon, Whites City. Here, the reef framework was dominated by very large individuals of the inozoan *Gigantospongia discoforma* (Pl. 3; Pl. 4, figs 2–3) and the sphinctozoan



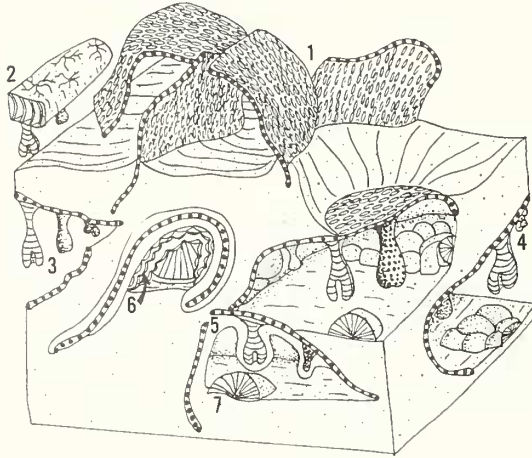
TEXT-FIG. 3. Tracings of serially slabbed polished surfaces (A-E) from the frondose bryozoan-sponge community cut perpendicular to horizontal from the Middle Capitan Limestone, McKittrick Canyon. STC-1-PmTx to STC-5-PmTx (corresponding to A-E respectively). Slabs are spaced approximately 15 mm apart. Note that frondose bryozoans commonly define crypt ceilings and walls, together with the platy sphinctozoan *Guadalupia zitteliana*. This framework was colonized by abundant cryptic sphinctozoan sponges. Both the reef framework and attached cryptos is enclosed by a post-mortem microbial micrite encrustation. A three dimensional reconstruction is given showing the convoluted nature of the bryozoan frond latticework. Scale bar represents 0.1 m.



TEXT-FIG. 4. Tracing of a weathered surface perpendicular to horizontal of the frondose bryozoan-sponge community from the Middle Capitan Limestone. Stop 15, elevation approximately 1905 m (6250 ft), Permian Reef Geology Trail, McKittrick Canyon. Note the lattice arrangement of the frondose bryozoans which commonly support crypt ceilings and walls, attendant cryptic calcified sponges, and encrusting nature of the microbial micrite. Modified from Wood *et al.* (1994). Scale bar represents 50 mm.

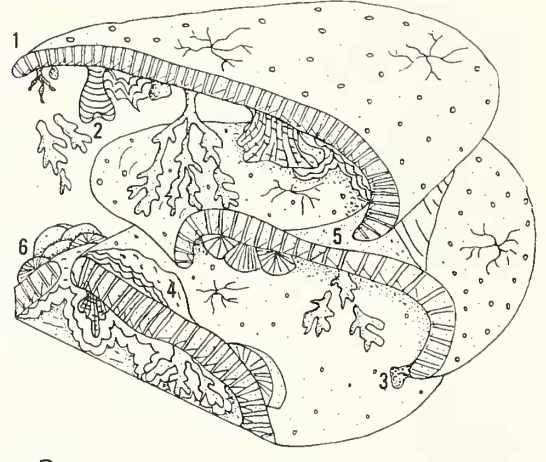
Guadalupia explanata, *G. discoforma*, although never more than 20 mm thick, grew up to 2 m in diameter. This species has also been found at Chinaberry and Hackberry Draws in the Guadalupe Mountains (Rigby and Senowbari-Daryan 1996). The less abundant *Gu. explanata* has a similar thickness, but reached a maximum diameter of 0.5 m. These sponges display laminar, convex, or convoluted morphologies, sometimes with marked downturned edges forming tunnel-like structures (Pl. 3, fig. 3). They were presumably attached by a site of limited size; no evidence of stacking, or mutual attachment of these platy sponges has been found. Microporous inhalant surfaces are on the underside and upper surfaces may bear traces of exhalant astrorhizal systems (Senowbari-Daryan 1990; Rigby and Senowbari-Daryan 1996). This orientation is constant in the field suggesting that these sponges are preserved in life position.

Frondose bryozoan-sponge community



A

Platy-sponge community



B

TEXT-FIG. 5. Schematic community reconstructions. A, frondose bryozoan-sponge community: 1, frondose bryozoans; 2, platy sponge (*Guadalupia zitteliana*); 3, cryptic solitary sphinctozoans; 4, cryptic nodular bryozoans; 5, microbial micrite + bioclastic sediment; 6, *Archaeolithoporella*; 7, aragonitic cement botryoids. B, platy sponge community: 1, platy sponges (*Gigantospongia discoforma* + *Guadalupia zitteliana*); 2, cryptic sphinctozoans; 3, cryptic bryozoans; 4, *Archaeolithoporella*; 5, microbial micrite; 6, aragonitic cement botryoids. Scale bars represent 1 m.



TEXT-FIG. 6. Rose diagram showing preferential alignment of cryptic sphinctozoan sponges taken from tracing shown in Text-figure 4. Only sponges whose growth direction could be determined were included.

EXPLANATION OF PLATE 2

Photomicrographs of the Permian Capitan reef.

Fig. 1. Frondose bryozoan-sponge community, Middle Capitan Limestone, McKittrick Canyon, showing the sphinctozoan *Guadalupia zitteliana* forming a cavity ceiling. The undersurface has been colonized by various encrusters including soft-bodied or weakly calcified forms, and the solitary sphinctozoan *Cystauletes*, upon which botryoidal cement fans have nucleated; SMX 26221; $\times 6$.

Fig. 2. Platy sponge community, Upper Capitan Limestone, Walnut Canyon, showing two cryptic pendent *Girtypora* sp. bryozoans, later encrusted by *Tubiphytes* and *Archaeolithoporella*; SMX 26222; $\times 10$.

Fig. 3. Frondose bryozoan-sponge community, Middle Capitan Limestone, McKittrick Canyon, showing the frondose bryozoan *Goniocladia* sp. forming a cavity. The crypt is inhabited by a fisuliporid bryozoan; SMX 26223; $\times 5$.

Fig. 4. Frondose bryozoan-sponge community, Middle Capitan Limestone, McKittrick Canyon. Peloidal texture and encrusting foraminifera of putative microbial micrite; SMX 26224; $\times 15$.

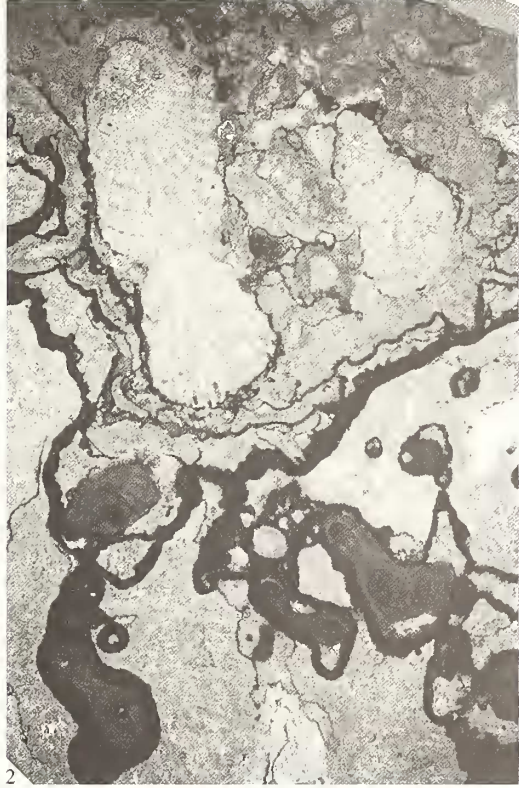


TABLE 1. Epibenthos identified within the frondose bryozoan-sponge community.

Open surface	Cryptos
Algae	Algae
<i>Archaeolithoporella</i>	<i>Archaeolithoporella</i>
Porifera	Porifera
Spinctozoans	Spinctozoans
<i>Guadalupia zitteliana</i>	<i>Girtycoelia</i> spp.
	<i>Guadalupia explanata</i>
	<i>Lemonea cylindrica</i>
	<i>Amblysiphonella</i> spp.
	<i>Cystauletes</i> spp.
	<i>Cystothalamia</i> sp.
	Hexactinellida
	?
	Cnidaria
	Rugosa
	<i>Lopophyllidium?</i> sp.
Bryozoa	Bryozoa
<i>Acanthocladia</i> spp.	<i>Girtypora</i> sp.
<i>Fenestella</i> spp.	<i>Fistulipora</i> sp. 1
cf. <i>Polypora</i> sp.	<i>Fistulipora</i> sp. 2
<i>Goniocladia</i> sp.	<i>Fistulipora</i> sp. 3
	<i>Acanthodema</i> sp.
	Echinodermata
	Crinoidea
	?
Problematica	Problematica
<i>Tubiphytes</i>	<i>Tubiphytes</i>
	Unidentified massive encruster
	<i>Microborers</i>

These platy sponge communities are found only in bathymetrically shallow parts of the Capitan reef, where the sponges appear to have grown either perpendicular to the reef front out into ambient currents, or perhaps formed a series of domes or tunnels towards the top of the reef. These sponges formed the ceilings of huge open crypts up to 2 m in height and width (Text-fig. 7).

In McKittrick Canyon, the platy sponges were colonized by a cryptic community of small solitary spinctozoan sponges and small, nodular bryozoans (Pl. 4, figs 1, 4). Rare macroborings are found in the cryptos.

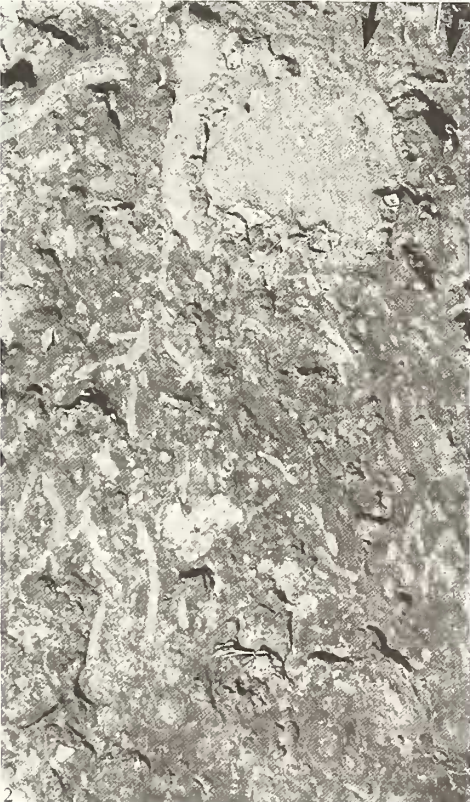
EXPLANATION OF PLATE 3

Platy sponge community

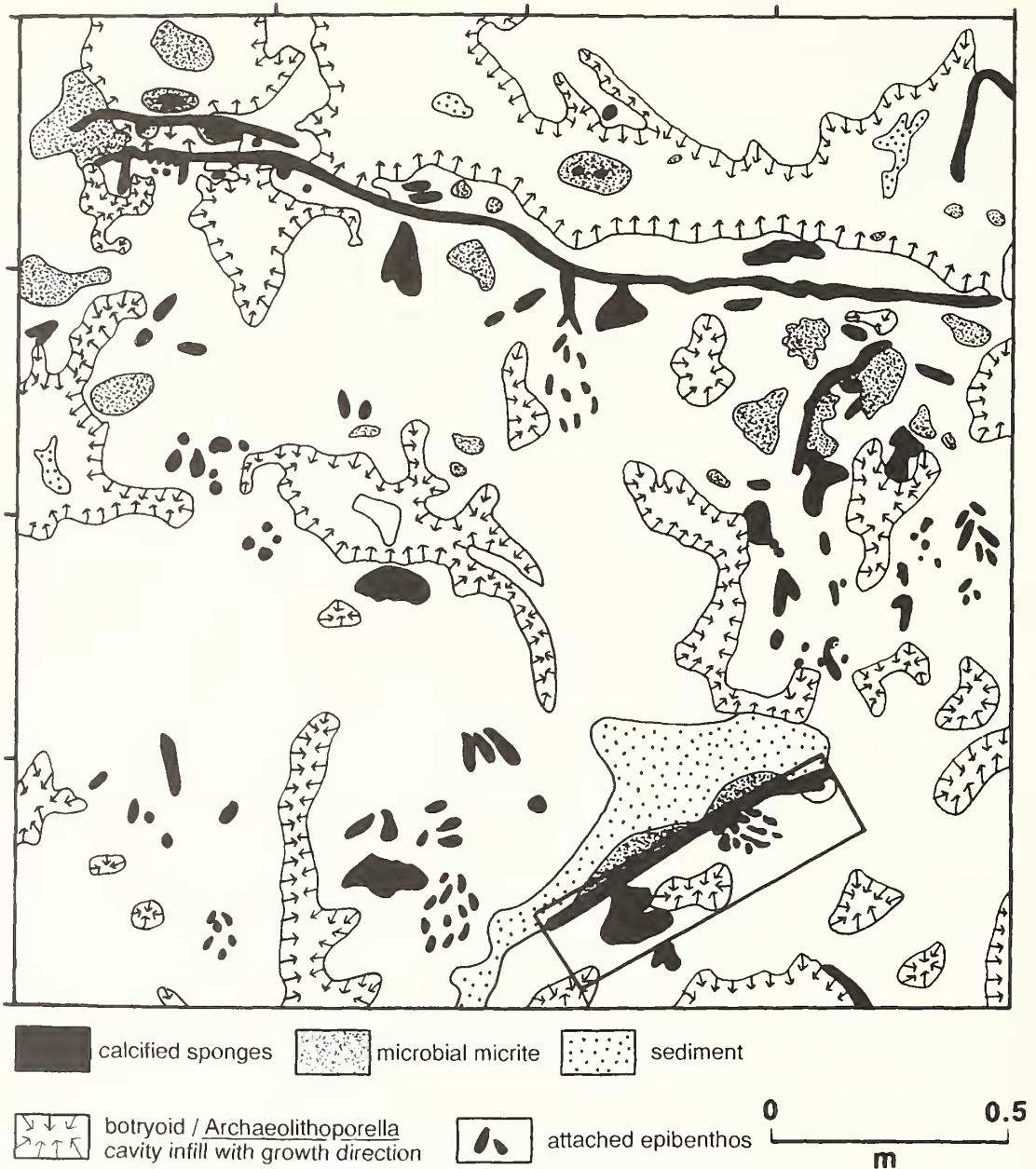
Fig. 1. Large individual of branching *Lemonea* sp. attached to the undersurface of *Gigantospongia discoforma*. Note attached crinoid stem (C) and bryozoan (B); $\times 0.67$.

Fig. 2. Extensive cavity ceiling formed by *Gigantospongia discoforma* (arrowed) supporting an extensive cryptos, including a branching individual of *Lemonea* sp. (left) and the compound *Guadalupia explanata* (right); $\times 0.2$.

Fig. 3. Detail of cryptos under *Gigantospongia discoforma*, including large sponge (S) and many bryozoans (B). Note encrustation of *Archaeolithoporella* on upper surface of *G. discoforma* and around the cryptos. Remaining cavity is filled with cement botryoids (I); $\times 0.67$.



WOOD *et al.*, platy sponge community



TEXT-FIG. 7. Tracing of weathered surface approximately perpendicular to horizontal showing the development of large cavities and cryptic communities under the large platy inozoan sponges *Gigantospongia discoforma*, Walnut Canyon, Whites City, Upper Capitan Limestone. Inset is enlarged in Text-figure 8.

At Walnut Canyon, the undersurfaces of the platy sponges were colonized by a diverse cryptic community (Table 2) dominated by large sphinctozoan sponges (Text-figs 7-8; Pl. 3; Pl. 4, fig. 2). Compound sphinctozoans (e.g. *Lemonea conica*) grew up to 0.25 m in diameter (Pl. 3, fig. 2; Pl. 4,

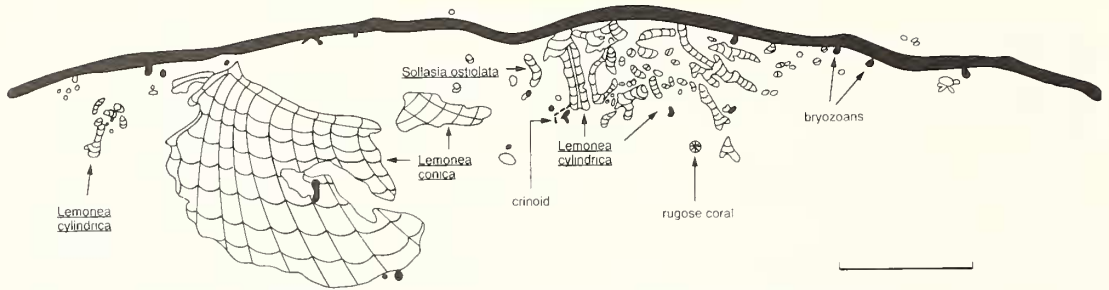
TABLE 2. Epibenthos identified within the platy sponge community.

Open surface	Cryptos
Algae	Algae
<i>Archaeolithoporella</i>	<i>Archaeolithoporella</i>
<i>Renalcis?</i>	<i>Renalcis?</i>
Porifera	Porifera
Sphinctozoans	Sphinctozoans
<i>Guadalupia explanata</i>	<i>Girtycoelia</i> spp.
	<i>Guadalupia explanata</i>
	<i>Lemonea cylindrica</i>
	<i>Lemonea conica</i>
Inozoans	<i>Lemonea polysiphonata</i>
<i>Gigantospongia discoforma</i>	<i>Lemonea</i> sp.
	<i>Parauvanella minima</i>
	<i>Discosiphonella mammosa</i>
	<i>Sollasia ostiolata</i>
	<i>Corymbospongia? pernica</i>
	<i>Amblysiphonella</i> sp.
	Cnidaria
	Rugosa
	<i>Lopophyllidium?</i> sp.
	Byozoa
	<i>Acanthocladia guadalupensis</i>
	<i>Girtypora</i> sp.
	<i>Fistulipora</i> sp. 1
	<i>Fistulipora</i> sp. 2
	<i>Fistulipora</i> sp. 3
	Echinodermata
	Crinoidea
	?
Problematica	Problematica
<i>Tubiphytes</i>	<i>Tubiphytes</i>
	Macroboers
	Microborers

figs 2–3) and branching sphinctozoans (e.g. *Lemonea* sp.) up to 0.5 m long (Pl. 3, fig. 2). Branching acanthocladid bryozoan colonies up to 0.4 m long are also present. Small, nodular bryozoans are found attached either directly to the undersurfaces of the platy sponges (Text-fig. 8; Pl. 3, fig. 3), or nestled amongst the larger members of the cryptos together with small rugose corals and crinoids (Pl. 3, fig. 1; Text-fig. 8).

The upper surfaces of the platy sphinctozoans and cryptic community were thickly encrusted by generations of often intergrown foraminiferans, *Tubiphytes* and *Archaeolithoporella* (Pl. 3, fig. 3; Pl. 4, fig. 1). In Walnut Canyon, the community was patchily enveloped on both upper, open and lower cryptic surfaces by a poorly preserved greenish-grey micrite with a peloidal fabric resembling the calcified cyanobacteria *Renalcis* (Text-fig. 7; Pl. 4, fig. 3). This micrite is estimated to occupy less than 10 per cent. of the total reef fabric volume.

The considerable remaining pore space was infilled by small botryoids (7–20 mm radius) and intergrown *Archaeolithoporella*, followed by large brown botryoids (30–60 mm radius) alone. As in the frondose bryozoan-sponge community the botryoids nucleated on the crypt ceilings, walls and floors as well as from the projecting cryptos. Some minor geopetal infilling of coarse, bioclastic sediment is present (Text-fig. 7).



TEXT-FIG. 8. Tracing of weathered surface approximately perpendicular to horizontal, showing the development of an extensive cryptic community beneath a large platy individual of *Gigantospongia discoforma*. Upper Capitan Limestone, Whites City. Scale bar represents 0.1 m.

From these observations we infer the sequence of development of the platy sponge community to have been:

1. The growth of large, platy sponges which projected horizontally from the reef slope or formed tunnels towards the reef crest (Text-fig. 5B).
2. The undersurfaces of the largest platy sponges were colonized by an abundant cryptos dominated by large, pendent sphinctozoans (Table 2).
3. The upper surfaces of the sponges and cryptic epibenthic community were thickly encrusted by foraminifers, *Tubiphytes* and *Archaeolithoporella*.
4. The entire reef community was enveloped by a patchy growth of microbial micrite.
5. Cavity space was filled mainly by the syn-sedimentary intergrowth of aragonitic botryoids and *Archaeolithoporella*, and later by large botryoids alone.

TROPHIC RECONSTRUCTION

Text-figure 9 reconstructs the inferred trophic relationships between the community elements of the Capitan reef biota. Three broad trophic groups are distinguished: primary producers, primary consumers and predators.

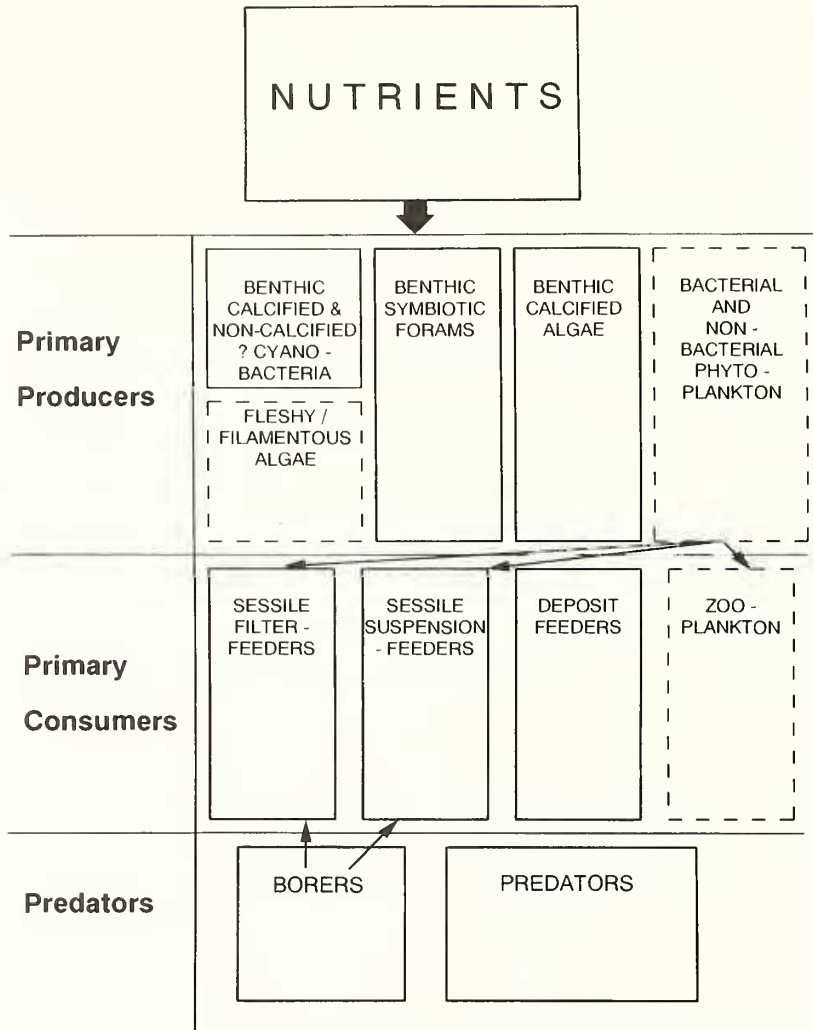
Bacterial, phyto- and zooplankton are inferred to be present, but their relative importance is not known. Several supposed benthic primary producers are present: putative photosymbiotic fusulinid foraminiferans, calcified cyanobacteria (e.g. *Collenella*?) and possibly the putative red algae (e.g. *Archaeolithoporella*). These elements were volumetrically minor components of the biota with the exception of *Archaeolithoporella*, which was predominantly cryptic. The peloidal fabric of the encrusting micrite suggests a bacterial origin; the originators may have possessed photosynthetic

EXPLANATION OF PLATE 4

Platy sponge community

- Fig. 1. Detail of fallen block in reef foreslope, McKittrick Canyon, inferred to be derived from the shallowest part of the Middle Capitan, showing the platy sphinctozoan *Guadalupia zitteliana* with cryptic bryozoans (arrowed), and *Archaeolithoporella* and intergrown botryoid encrustations on both upper and lower surfaces; $\times 1$.
- Fig. 2. Etched surface of Upper Capitan Limestone from the mouth of Walnut Canyon, showing a tangential section through individuals of the cavity-forming platy sponge *Gigantospongia discoforma* and attendant solitary and branching cryptic sphinctozoans; lens cap diameter = 55 mm.
- Fig. 3. Etched surface of Upper Capitan Limestone from the mouth of Walnut Canyon, showing large compound sphinctozoan *Lemonea conica* and other sphinctozoans attached to undersurface of *Gigantospongia discoforma*. Note patchy encrustation of ?microbial micrite (arrowed); $\times 0.25$.
- Fig. 4. Fallen block in reef foreslope, McKittrick Canyon, showing stacking of the platy sphinctozoan *Guadalupia zitteliana*; lens cap diameter = 55 mm.





TEXT-FIG. 9. Trophic web reconstruction of the Permian Capitan reef ecosystem. Inferred categories are shown in dashed boxes.

capabilities. Fleshy and filamentous algae were most probably present, but were probably not volumetrically significant as few herbivores (with the possible exception of some gastropods) are recognized. There is no evidence to suggest therefore that benthic primary producers were trophically closely linked to primary consumers. The solitary and low-integration branching organization of most sphinctozoan sponges, their inferred internalized soft-tissue, as well as their cryptic habit indicates that they did not bear photosymbionts. Although the high-integration modular sponges such as *Gigantospongia discoformis* and *Guadalupia explanata* reached a very large size, there is also no evidence of either externalized soft tissue or the fast rates of growth or heavy calcification that might be expected in photosymbiotic forms.

The majority of the sessile Capitan reef metazoans were primary consuming heterotrophs. We distinguish between filter feeders capable of effective use of non-aggregated bacterial plankton and suspension feeders capable of capturing aggregates only. The most abundant element of the sessile community of primary consumers were sessile filter feeders; sphinctozoan, inozoan and spicular

sponges. The main diet of living sponges is planktonic bacteria (Reiswig 1974), and these bacteria also serve as the main food source for small cnidarians (Sorokin 1990) represented here by relatively uncommon rugosan and tabulate corals. Suspension feeders are represented by abundant brachiopods, bryozoans, crinoids and bivalves. Over 46 brachiopod species and 12 bryozoan species have been identified from the Capitan Limestone (Newell *et al.* 1953).

Inferred deposit feeders are represented by four species of gastropod and one species of trilobite. Other minor representatives of the fauna are scaphopods (one species), ammonoids (one species) and nautiloids (three species) (Newell *et al.* 1953). Scaphopods were probably slow-moving epifaunal detritophages, whilst the nautiloids and ammonoid may have been predators. This nekton may, however, have been part of the open water fauna of the Delaware Basin and not trophically closely linked to the reef. There is also rare evidence of macro- and microboring activity.

The Capitan community is thus notable for the proliferation of heterotrophic primary consumers, relatively little development of benthic calcified phototrophs and the absence of significant numbers of predators. This infers the presence of abundant suspended food matter presumably mainly in the form of plankton. Relatively high nutrient levels can thus be inferred to have been present in the Delaware Basin. Also, the waters were presumably devoid of much suspended sediment which would clog filter- and suspension-feeding mechanisms. Similar conclusions were reached by L. C. Babcock (1974), J. A. Babcock (1977) and Yurewicz (1977).

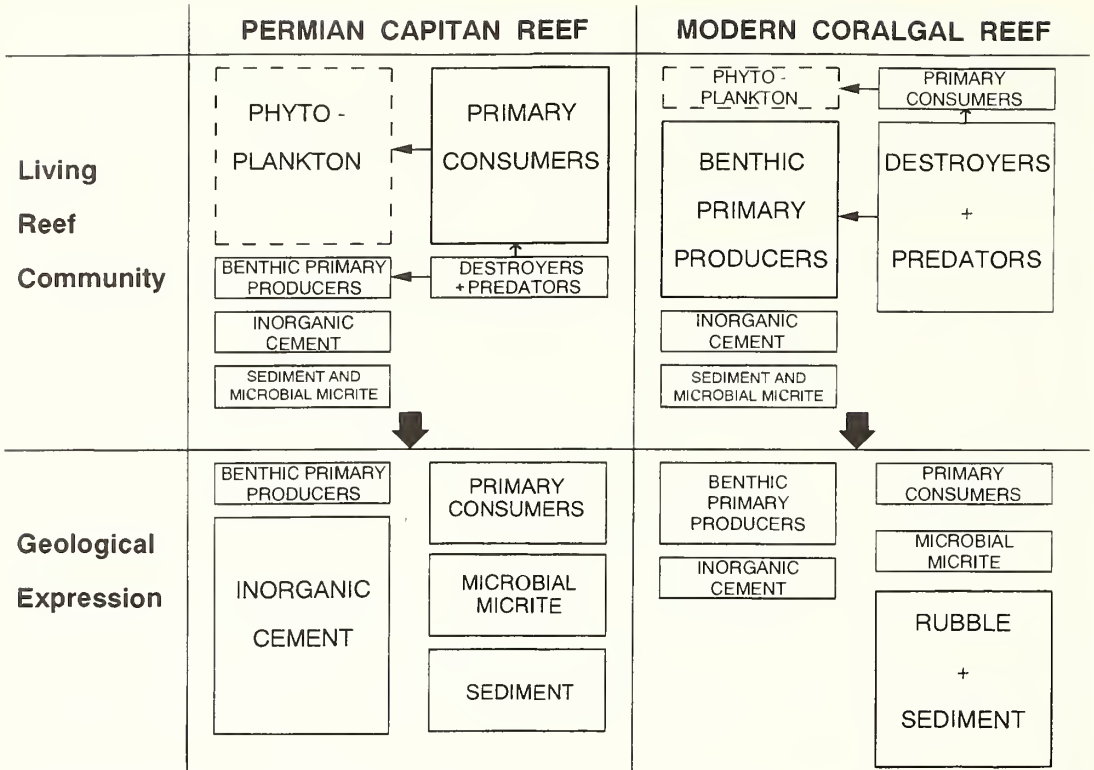
PRODUCTIVITY AND CARBONATE BUDGET

The Capitan Limestone ranges from 100 to 200 m thick and during the late Guadalupian interval (some 2.5 My) prograded 19 km basinwards on to the north central shelf. Estimates for the rate of the reef margin aggradation are 3.3–7.7 mm/yr during Lower Capitan time, and 1.1–2.6 mm/yr during the Middle and Upper Capitan (Garber *et al.* 1989: all figures neglect differential compaction). This yields an average rate of accumulation of 3–4 mm/yr giving the Capitan Limestone one of the most rapid accumulation rates of any known Phanerozoic carbonate platform (Garber *et al.* 1989). These rates compare well with modern reef accumulation, which is estimated to be an average of 3–4 mm/year (Buddemeier and Hopley 1988).

Such comparable rates of accumulation, however, mask substantially different relative contributions of organic and inorganic carbonate to the final reef fabric which result from profound differences in the ecology of the Permian Capitan reef compared with modern coralgal reefs. Modern coralgal reefs thrive in low nutrient seas and not surprisingly net planktonic primary productivity is estimated to be low: only one-tenth of the net benthic primary productivity (Grigg *et al.* 1984). Most productivity is derived from heavily calcified benthic coralline algae and photosymbiotic scleractinian corals.

The benthically dominated modern reef ecosystem is regulated by intense predation which controls higher trophic production. Modern reefs have exceptionally high levels of ecotrophic efficiency, with estimates indicating that between 50–85 per cent. of a species' annual production is consumed by predation or herbivory (Grigg *et al.* 1984). This high internal predation exists mainly between the heterotrophic benthos and reef fish. The effect of suitable habitat availability, which in turn determines the amount of photosynthetically active area, is also a major control in the gross primary production of modern reefs, and indeed may even be a limiting factor (Grigg *et al.* 1984; S. V. Smith 1981). Were similar constraints and controls also present during the Permian?

The trophic structure of the modern coralgal reef is profoundly different to that reconstructed for the Permian Capitan ecosystem (Text-fig. 10). Relatively few putative calcified photosynthesizers have been recognized in the Capitan: only a small proportion of overall productivity appears to have been present in the benthic photosynthetic community. Indeed, the calcified benthos is volumetrically dominated by heterotrophs, most of which were cryptic. To support such a rich community of primary consumers, it is necessary to infer high levels of plankton and therefore nutrients in the Delaware Basin. In addition, very few possible predators have been recognized and boring activity, although present, was extremely sparse.



TEXT-FIG. 10. Comparison of the relative volumetric contribution of different elements of the reef biota and associated inorganic sources of carbonate in the Permian Capitan and Recent coralgall reefs, in the living reef communities and in their geological expression. The Permian reef framework, whilst showing no evidence of a high degree of wave resistance, remained intact due to the absence of any significant numbers of destroyers and predators. Original crypts were thus preserved and became infilled with substantial volumes of inorganic cement. In contrast, the abundant predators and destroyers on modern coralgall reefs rapidly reduce the framework to mainly rubble and sediment.

The abundant herbivores and predators not only serve to regulate the trophic structure of modern coralgall reefs, but also rapidly reduce the otherwise robust framework to between 40–90 per cent rubble and sediment (Hubbard 1989) by boring, rasping, etching and excavating activity. Otherwise intact framebuilders as well as reef rubble are commonly riddled extensively with borings such that the original reef-building framework is often totally obliterated (Macintyre 1977). Yet many of the abundant herbivorous, predatory and destructive elements did not appear in quantity until the mid-Mesozoic onwards – a radiation event known as the Mesozoic Marine Revolution (Vermeij 1977, 1987). In particular, the major groups of herbivorous and predatory fish on modern reefs did not appear until the Eocene.

We therefore suggest that the apparently fragile, but cavernous Permian reef framework, showed no evidence of physical destruction and hence substantial wave resistance, and remained intact largely due to the absence of significant numbers of predators and destroyers in the ecosystem. Original crypts were thus preserved firstly by encrustation (calcified encrusters and microbial micrite) and possibly pervasive microscopic cementation, and later by extensive infilling of crypts by inorganic cement. In contrast to modern reefs, where the overwhelming bulk of carbonate is organically derived and photosynthetically boosted (Barnes and Chalker 1990), a substantial

proportion of Capitan reef carbonate is thus contributed by inorganic cement processes (Text-fig. 10).

We conclude that before the Mesozoic Marine Revolution relatively fragile reefs could be preserved in areas where intense syndimentary cementation processes were active – in moderate- to high-energy environments with high rates of flushing. We therefore must consider Palaeozoic reef frameworks in a new light – the presence of either an intact fossil reef framework or similar rates of carbonate accumulation cannot infer that a fossil community grew under the same conditions as do modern reefs.

DISCUSSION

Differentiation of the biota

Reefs have been strongly differentiated into distinctive open surface and cryptic communities since their inception, although the identification of cryptic communities is frequently overlooked in palaeoecological analyses. Where studied, it has been shown that fossil reef crypts have often housed a substantial proportion of overall biodiversity (e.g. Kobluk 1988; Wood *et al.* 1993; Zhuravlev and Wood 1995). In modern coralgal reefs, open surface communities are dominated by phototrophic organisms—mainly coralline algae together with photosymbiotic metazoans. In contrast, filter and suspension-feeding organisms predominate in cryptic niches (Jackson and Buss 1975; Jackson 1977; Jackson and Winston 1982; Choi and Ginsburg 1983; Choi 1984). Encrusting sponges and bryozoans are abundant as they appear to be the best overgrowth competitors (Jackson and Winston 1982), but solitary organisms, such as serpulids, foraminiferans and brachiopods, are also conspicuous elements, even though they occupy little space (Jackson 1977).

Crypts provide niches well protected from direct exposure to local environmental pressures, such as wave scour, intense irradiation and predation. Unoccupied substratum is rare in crypts and overgrowths are frequent, suggesting that like the open surface, competition for space is intense. Nutrient supply and oxygen availability (provided by sufficient water flow) are critically important to modern cryptic communities (Kobluk and James 1979).

The two new Capitan reef communities here described represent a substantial proportion of the total discernible reef fabric in the Middle and Upper Capitan Limestone. Both communities display a previously unrecognized marked differentiation of the sessile calcified epibenthos into distinct open surface and cryptic communities (see Tables 1–2). Indeed, most of the overall diversity of the skeletal epibenthos of the Capitan reef was housed within the crypts and, remarkably, most of the cryptic metazoans identified were obligate cryptobionts. Micrite-producing microbial communities appear to have been equally abundant on both the open and cryptic surfaces of the platy sponge community, but *Archaeolithoporella* grew predominately within crypts in both communities. Although sediment fills within crypts commonly contain abundant bioclastic debris (such as trilobite segments) as well as whole fossils (e.g. brachiopods and gastropods), we have not been able to exclude current sorting as a mechanism for the enrichment of these vagile organisms within crypts, and have therefore excluded them from our analyses.

The Capitan reef therefore differs from many described fossil reef ecologies in that most of the skeletal epibenthos was composed of obligate cryptobionts. This deserves explanation. Either ambient current energies were too high to favour the growth and/or preservation of these organisms on the exposed open surfaces, or these surfaces were covered by competitively superior, encrusting soft-bodied epibenthos. Because there is little evidence of significant numbers of herbivores in the Capitan ecosystem, this open surface community is unlikely to have been predominantly algal. Likewise, the absence of abundant spicules within crypt infill suggests that sponges did not form a substantial part of any soft-bodied community.

There is ample evidence that competition of cryptic surfaces in the Capitan was intense, as numerous examples of multiple encrustation and chains of several individuals have been observed (Pl. 2, fig. 1; Pl. 3, figs 1, 3). As on modern reefs, hard substrate was apparently at a considerable premium. In the Recent, solitary organisms tend to be poor space competitors on hard substrates as

they generally have small areas of attachment and lack specific competition mechanisms (Jackson 1977, 1985). Many solitary organisms do commonly occur, however, in modern cryptic habitats (Jackson 1977).

In both modern and fossil reef crypts, the size of cryptobionts appears to be related to the size of the crypt and time available for colonization (Zhuravlev and Wood 1995). The two cryptic populations in the frondose bryozoans-sponge and platy sponge communities are not only notably systematically different (see Tables 1–2), but differ also in terms of individual size and functional morphology. The cryptic sphinctozoans found in the frondose bryozoan community tend to be relatively small, solitary forms (usually 50–100 mm long), whilst those in the huge crypts of the platy sponge community display modular organizations (branching uniserial and compound multiserial) with individuals sometimes reaching 0.5 m in length. The vast majority of cryptobionts, however, including the multiserial sphinctozoans, bear notably small attachment sites (e.g. Pl. 1, figs 1, 3; Pl. 2, fig. 2; Pl. 3, fig. 2).

The ratio of modular to solitary species is proposed to be a function of substrate longevity (Jackson 1985) and indeed studies on community development in modern reefal crypts demonstrate that over time an ecological succession takes place from solitary to modular encrusting organisms (e.g. Choi 1984). The distribution of these different morphologies in the two described Capitan cryptic communities might therefore reflect this dynamic, but the expected succession from solitary to modular organizations is not observed in the large platy sponge community where it might be predicted. Surface area and volume were clearly variable in the Capitan crypts, and were determined by the size of the individual framebuilders. Indeed framebuilders not only determined the size of the crypts, but also the length of time the crypts were available for colonization: the large, relatively stable and presumably long-lived large platy inozoan sponges display noticeably larger cryptobionts than those inhabiting crypts formed under the smaller, more fragile frondose bryozoans. The larger average size of the botryoid cements within the crypts formed by the platy sponges also suggests that these crypts remained open for longer. That this community appears to have grown in more shallow, and probably more agitated waters may also be significant.

Interestingly, modern cryptic surfaces are dominated by multiple encrustations which are essentially two-dimensional (Jackson 1985). This is in stark contrast to the highly pendent and three-dimensional character of the Capitan reef crypts. Modern solitary organisms appear to be more dependent upon disturbance processes to provide suitable sites for settlement and growth than modular encrusting organisms, presumably because they are poorer competitors for space. Their generally small size, rapid growth rates and short generation times favour generalist, opportunist, or fugitive life strategies (Jackson 1977). Relatively few calcified multiserial encrusting organisms, however, were present in the late Palaeozoic compared with the mid-Palaeozoic, Mesozoic and Recent (Taylor 1990). In the absence of more efficient space competitors therefore, we might expect a greater dominance of pendent, solitary, calcified metazoans in the crypts during the Late Permian.

Large cryptic niches such as caves, grottoes and crevices have long held a celebrated status as refuges for faunas of an ancient caste. Modern reefal caves house putative relict communities of Mesozoic reef-building calcified demosponges ('sclerosponges') including sphinctozoans, and thecidian brachiopods (Jackson *et al.* 1971). Chambered sponges appear to have commonly inhabited a cryptic niche through the Palaeozoic (Wood *et al.* 1994; Zhuravlev and Wood 1995). Chambered archaeocyath sponges were common cryptobionts in Lower Cambrian reefs, as were Ordovician sphinctozoans from Koryakia, Russia and Silurian aphasalpingids from Alaska and the Urals. Several groups of Palaeozoic chambered calcified sponges, previously interpreted as erect reef framebuilders, may in fact have been preferential crypt dwellers (Wood *et al.* 1994). Chambered calcified sponges exhibit varied morphologies, but most have small attachment sites. Such organizations conferred better competitive abilities within crypts than on open surfaces, where they would have been outcompeted by modular, encrusting organisms with an ability both to cover and occupy new substrate rapidly.

Importance of bryozoans in ancient reefs

The framebuilding importance of frondose bryozoans in the Capitan reef represents a radical departure from the established ecology. Modern bryozoans flourish principally between 10–80 m depth in oxygenated waters of normal salinity, clarity and moderate agitation, and in temperatures between 20–28 °C. Bryozoans in some Palaeozoic reefs constructed a semi-rigid lattice which created a framework for the settlement of other sessile, dwelling organisms (Cuffey 1974, 1977; Zimmerman and Cuffey 1987). Bryozoans also performed complementary roles of sediment baffling and trapping by encrusting or binding.

Bryozoans, especially fenestellids, have been described as major framebuilders in a number of reefs, e.g. the Mississippian of south-western USA (Pray 1958), the Dinantian of Ireland (Philcox 1971) and the Upper Permian reef of north-eastern England (D. B. Smith 1981*a*, 1981*b*). Bryozoans also played a supportive role in some Silurian reefs: Scoffin (1971, 1974) noted that the framework of Wenlock reefs in Shropshire consists mainly of bryozoans encrusted by stromatolites and partially infilled by micrite internal sediment. In some areas, fenestellid bryozoans formed the roofs of small cavities (1974: see fig. 4, p. 570).

Many Permian reefs display abundant bryozoans, both frondose and erect branching pinnate forms. Schwarzhacher (1961) serially sectioned reef limestone from the Lower Carboniferous of Ireland and demonstrated the presence of a growth lattice of fenestellid fronds, although he found no evidence for interconnections between colonies. Small bryozoan frame-thicket bioherms grew in deep waters, especially during the late early Permian and latest mid Permian, along the southern margin of the Delaware Basin (Zimmerman and Cuffey 1987). Etched material from the Glass Mountains reveals silicified bryozoan frameworks. Here, small bioherms consist of fenestrate and pinnate (most notably *Acanthocladia* spp.) zoari attached and intertwined, thereby creating a scaffolding with some structural rigidity (Zimmerman and Cuffey 1987). Calcified sponges, as well as brachiopods and fistuliporids, dwelt within the framework. Likewise, one of the dominant framebuilders in the Upper Permian reef of north-eastern England is also a species of *Acanthocladia* (D. B. Smith 1981*a*, 1981*b*). Babcock *et al.* (1977, p. 29) also illustrated frondose 'fenestellid' bryozoans from the Middle Capitan Limestone, McKittrick Canyon, creating what were interpreted as depositional shelters.

The apparent fragility of frondose bryozoans may be misleading in that their many fenestrule openings permitted water flow through the colony such that they could withstand quite strong currents (D. B. Smith 1981*a*). Frondose colonies also produced secondary thickening and were capable of lateral fusion and connection. McKinney and Gault (1980) deduced that most fenestellids lived in moderately energetic to relatively quiet waters, either near or below normal wavebase or in sheltered localities. Those with lyre-like growth morphologies could withstand more vigorous unidirectional currents. Indeed Elias and Condra (1957) considered that a conjoined lattice of fenestellids would be able to withstand turbulence when stiffened by a partial filling or coating of submarine cement or micrite.

Bryozoans predominantly inhabited open reef surfaces during the Palaeozoic (Cuffey 1974) but today they are more common in crypts (Kobluk *et al.* 1988). It has been suggested that they became predominantly cryptic during the Cenozoic (Cuffey 1974). Available evidence from calcified sponge groups, however, indicates that these modern cryptobionts are not displaced former open surface dwellers, but probably represent the remnants of communities which have always occupied cryptic niches. The evolution of light-dependency in scleractinian corals may have prompted the demise of open surface dwellers and restricted many calcified heterotrophs to the cryptos (Wood 1995).

Importance of microbial micrite and cement precipitation

Post-mortem microbial encrustation was clearly of considerable importance in the Capitan reef, especially in the frondose bryozoan-sponge community, in that it imparted considerable rigidity to an otherwise relatively fragile framework. Deposits of microbial micrite have been found extensively

in modern cryptic reef environments (e.g. Land and Moore 1980; Reitner and Neuweiler 1995). These studies suggest that the major control on micrite formation is the presence of Ca-binding organic matter. This has been found to often have its origin in decaying organisms, especially sponges and microbes. Crystal nucleation also requires increased carbonate alkalinity, which may be controlled by sulphate reduction in anaerobic layers of stratified water bodies (Reitner and Neuweiler 1995).

Locally, up to 70 per cent. (this study) or 80 per cent. (Schmidt 1977) of the Capitan reef may be occupied by marine cement. A similar volume of aragonitic marine cement has been estimated to be present within the bryozoan framework of the Upper Permian Magnesium reef, north-eastern England (Hollingworth and Tucker 1987). Indeed, large quantities of precipitated carbonates are globally common in the late Permian.

The Late Permian was a time of global low-stand in sea-level, and many authors have suggested the Late Permian ocean to have been stratified, with anoxic bottom waters (e.g. Margaritz and Turner 1982; Erwin 1994). This is supported by the unusual enrichment of ^{13}C in Late Permian carbonates, including those from the Capitan reef (e.g. Garber *et al.* 1989; Margaritz *et al.* 1992). Moreover, an alkalinity pump has been inferred to have controlled the amount of carbonate ions in the upper water masses (Margaritz and Turner 1982). The Zechstein and Delaware basins were also partially isolated from the world ocean, and both are thought to have been stratified with well-developed anoxic bottom waters which underwent periodic overturn (e.g. Newell *et al.* 1953; D. B. Smith 1981a; L. C. Babcock 1977; Margaritz and Turner 1982). The Delaware basin was probably sufficiently restricted so as to be particularly sensitive to continental runoff (Margaritz *et al.* 1983). All these phenomena would have favoured the precipitation of carbonate salts at the margins of the basins, especially where there was considerable flushing (Grotzinger and Knoll 1995).

Depth of formation, ecological zonation and bathymetric profile

The Capitan reef is one of the steepest known ancient prograding carbonate shelf margins. Existing erosional slope angles are usually 20–40°, whilst strata immediately landward of the reef have dips of 5–15°. The seaward slope on these so-called 'fall-in' beds has been taken by some (Hurley 1989) to be largely depositional and hence used to provide a measure of water depth over the reef, assuming that the fall-in beds were deposited up to sea-level. Others (e.g. Smith 1973; Newell *et al.* 1955) concluded that the seaward dip of the Capitan as well as the fall-in beds was the result of syndepositional or post-depositional tilting.

To resolve these competing hypotheses, Saller (1996) measured the strike and dips of geopetal surfaces in the Middle Capitan reef, McKittrick Canyon. He noted that such geopetal structures have a consistent basinward dip of 11° at an average azimuth of 130° (S50° E), which indicated a post-depositional basinward tilting of the Capitan at an angle perpendicular to the depositional strike of the Capitan reef in the area (40°; N40° E). Fall-in beds have similar basinward dips to geopetals in the Capitan reef. Saller (1996) thus concluded that differential compaction may have tilted the Capitan reef and fall-in beds when dense lithified reef and shelf carbonates prograded over the highly compactable lower-slope and basinal carbonate muds. Hence much of the apparent dip of the fall-in beds and reef should not be viewed as depositional and cannot be used explicitly to determine the depth at which the Capitan Limestone formed. These results would suggest that the depositional slope of the Capitan reef was in fact usually in the order of approximately 10–30°.

The Middle Capitan reef was dominated by the frondose bryozoan-sponge community, except for the uppermost 10 m of the reef. This community is also noted 13 m below the uppermost exposure of Upper Capitan Limestone at Walnut Canyon, marking the bathymetrically deepest community found in the Upper Capitan. The frondose forms which constructed the framework of the Middle Capitan show considerable secondary thickening and were capable of lateral fusion and connection. Although frondose bryozoan debris is noted in the Capitan reef, most of the bryozoan fronds are

intact. We consider that such a latticework would be able to withstand moderate turbulence, especially when stiffened by a partial filling or coating of submarine cement or micrite and further biological and microbial encrustation.

The Capitan reef is notable for the lack of zonation except in the bathymetrically most shallow parts. In modern coralgal reefs, well defined zones dominated by different scleractinian morphologies are present down to considerable depths on the reef front. Response to light availability, as well as wave energy, temperature and sediment input, is responsible for this zonation (Chappell 1980). Such a benthic phototrophic response has been recognized in only the most shallow parts of the Capitan reef: isolated colonies of the putative algae *Collenella* in the uppermost 10 m of Middle Capitan at McKittrick Canyon, branching *Tubiphytes* in the uppermost 5 m of Upper Capitan at Walnut Canyon and *Eugonophyllum* 13–10 m below the uppermost exposure at Walnut Canyon. This perhaps suggests that the remainder of the reef did not occupy the euphotic zone. Interestingly, D. B. Smith (1981a) also noted that the middle portions of the Upper Permian Magnesium reef, north-eastern England are characterized by an increase in the proportion of algae at the expense of bryozoans which were dominant in the earlier, possibly bathymetrically deeper, stages of reef growth. Modern reefs, being phototrophic, are restricted to the euphotic zone, and usually extend no deeper than 100 m. In contrast, the Capitan reef is thought to have reached some 150 m (Bebout and Kerans 1993).

The platy sponge community is restricted to bathymetrically shallow parts of the reef. In the Middle Capitan Limestone at McKittrick Canyon it occurs with *Collenella* towards the top of the reef. At Walnut Canyon, it forms a discrete horizon below the most shallow zone occupied by the *Tubiphytes*-sponge community. It appears to represent the lower part of the reef crest or the growing edge of the reef front itself.

The increased importance of putative algae in the Upper Capitan may indicate progressively more shallow growth of the reef. Alternatively, the uppermost parts of the Middle Capitan reef may not be preserved. The post-mortem microbial and inorganic lithifying processes acting upon the reef community were capable of forming a rigid structure, which, if growing in shallow waters, would have been capable of modifying the surrounding environment. Detailed study of the reef to shelf transition demonstrates that the reef did indeed modify the sedimentary processes that took place in its lee, and in so doing controlled sedimentation across the shelf (BLK, pers. obs).

SUMMARY

The Permian Capitan reef ecosystem was a highly differentiated community, where most of the sessile calcified epibenthic diversity was housed within the cryptos. Moreover, most members of the cryptos were obligate cryptobionts. Sponges in particular were markedly differentiated into both systematically and ecologically distinctive open surface and cryptic communities. Whilst open surface framebuilders were predominantly platy, multiserial forms, the cryptobionts, were rapidly establishing organisms with small attachment sites and solitary, branching and compound organizations. There is evidence of a soft-bodied cryptos and of intense competition for space, as cryptobionts commonly form multiple overgrowths and chains of individuals.

Cryptic habitats offered an alternative habitat of reduced environmental stress. However, unlike modern reefs, irradiation and predation were not important controls in the Capitan reef ecosystem. Except for microborings and rare macroboring, no evidence of biological destruction on the calcified benthos has been noted and very few predators have been recognized in the community. Benthic phototrophism was responsible for zonation only in the bathymetrically most shallow parts of the reef.

Unlike modern phototrophic coralgal reefs, the Capitan was a predominantly heterotrophic ecosystem, supported by inferred high levels of primary producing plankton in the Delaware Basin. Many workers (e.g. James 1983; Fagerstrom 1987; Kobluk 1988) have commented that truly cavernous, large-scale cavity systems did not appear in reefs until the appearance of large

TABLE 3. Comparison of the ecological characteristics of the Permian Capitan Reef and modern coralgal reefs. References: 1: Hubbard (1989); 2: James (1983); 3: Kirkland *et al.* (1993).

	Permian Capitan reef	Recent coralgal reefs
Major framebuilders	Heterotrophs: fenestellid bryozoans + platy calcified sponges	Mixotrophs, phototrophs: scleractinian corals + coralline algae
Volume occupied by organic framework in living reef (per cent.)	< 10	> 50
Volume occupied by inorganic framework in geological reef (per cent.)	> 40	< 10
Intact framework in geological reef (per cent.)	Up to 100	10–60 (1)
Wave energy	Low–medium	High
Destroyers and predators	Rare	Abundant
Zonation	Minimal	Marked
Maximum depth of reef front	Up to 150 m (3)	Up to 100 m (2)

phototrophic scleractinian corals in the Mesozoic. The Capitan reef, however, was a highly cavernous system, with large cavities up to 2 m in diameter in shallow parts.

Many studies of fossil reef communities have overemphasized the importance of massive framebuilders: the Capitan reef formed in their absence and its sustained growth and preservation was due to post-mortem microbial encrustation and extensive early cementation. Microbial encrustation was especially important in the frondose bryozoan-sponge community, where it imparted considerable rigidity to an otherwise fragile framework. Without such processes, the reef would probably have evolved as a bioclastic bank. In addition, the cavernous Permian reef framework remained intact due to the absence of significant numbers of destroyers in the ecosystem and to its inferred growth below the turbulent zone. As a result, in contrast to modern reefs where the overwhelming bulk of carbonate is organically derived, a substantial proportion (up to 70 per cent.) of Capitan reef carbonate (as exposed) is contributed by inorganic cement. Table 3 summarizes the ecological differences between the Permian Capitan and modern coralgal reefs.

Several groups of Palaeozoic chambered calcified sponges, previously interpreted as erect reef framebuilders, may in fact have been preferential crypt dwellers (Wood *et al.* 1994; Zhuravlev and Wood 1995). Such organizations, with their small attachment sites, may have been better competitors within crypts than on open surfaces, where they would have been outcompeted by high-integration, encrusting organisms with an ability to cover and occupy new substrate rapidly.

The ecological interpretations presented here represent a radical departure from the established descriptions. They are not, however, intended to present a complete review of the ecology of the Capitan reef: rather to offer a new frame of reference in which further observations can be placed.

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